21

An Experimental Study of the Color Vision of the Giant Tortoise

JOHN V. QUARANTA

Research Associate, New York Zoological Society;
Department of Psychology, Manhattan College, New York City[1]

(Plates I & II; Text-figures 1 & 2)

CONTENTS

INTRODUCTION

EXPERIMENTAL studies of color vision in Reptilia have been carried out by a number of investigators on a wide variety of species, employing experimental procedures that are as diversified as they are questionable. Investigations devoted to Chelonia and Squamata are more numerous than those devoted to Ophidia and Crocodilia and, from a qualitative point of view, are also better designed and controlled.

The present investigation was undertaken to determine whether, among chelonians, the Giant Tortoise is capable of basic discrimination among red, green and blue light targets. All work was done in the New York Zoological Park.[2]

The basic problem investigated in the present experiments was inspired by the "modulator-dominator theory" evolved by Ragnar Granit (1947) during the years 1930-1945.

Granit has considered the modulator curves (narrow response curves peaked at different points in the spectrum) to be indicators of capability on the part of the animal for color discrimination. Difficulty with this interpretation has arisen because these modulator curves have been found in animals which generally have been regarded by psychologists as lacking color discrimination, for example, the cat and the rat. Granit's hypothesis would be more readily acceptable if his interpretation were strengthened by experimental evidence that on the behavioral level animals showing these modulator curves actually do discriminate color. A review of the literature of the vertebrate eye in general, and of the reptilian eye in particular, shows that much is to be desired in the way of carefully controlled experiments (Detwiler, 1943; Walls, 1942). In view of the decided inadequacy of studies on reptilian color vision, the present investigation was undertaken. Substantiation of such inadequacy is revealed by the ensuing review of the literature together with a critical evaluation of the work reported.

LITERATURE OF THE SUBJECT, AND A CRITICAL EVALUATION

Studies of color vision in Chelonia have been conducted by Hess on *Cyclemys palustris*,

[1] Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Psychology at Fordham University, 1952.

[2] The writer wishes to express his sincere appreciation to Professors Joseph G. Keegan, S.J., and Richard T. Zegers, S.J., whose untiring patience and kindly interest were major factors in the completion of this work. His thanks are also due to the authorities of the New York Zoological Society. In particular they are extended to Mr. Fairfield Osborn, President; Mr. John Tee-Van, Director of the New York Zoological Park; Dr. Leonard J. Goss, Veterinarian; Mr. Lee S. Crandall, General Curator Emeritus; and to Dr. C. R. Carpenter, Coordinator of Animal Behavior.

These studies, in their beginning, received the strong encouragement of the late Brayton Eddy, Curator of Reptiles from 1945 to 1950.

Cyclemys trifasciata and *Geoclemys reevesi* (1910). Other studies have been carried out by Wojtusiak on *Clemmys caspica* (1932); by Wojtusiak & Mlynarski on *Emys orbicularis* and *Geoclemys reevesi* (1949); by Bartkowiak on *Emys orbicularis* and *Geoclemys reevesi* (1949); by Hooker on *Caretta caretta* (1911); by Kuroda on *Clemmys japonica* (1933); and finally, by Granit on *Testudo graeca* (1947). Studies of color vision in Lacertilia have been conducted by Wagner on *Lacerta agilis* and *Lacerta viridis* (1932); by Schlieper on *Lacerta vivipara* (1927); and by Swiezawska on *Lacerta agilis* (1949).

Studies of color vision in Ophidia are probably fewest and certainly the most inadequate. The paucity of such investigations can be attributed to the extreme difficulty encountered in conditioning and in working with these experimental subjects. Kahmann is reported to have obtained positive results in training an unidentified species to discriminate between red and blue (Walls, 1942). The sensitivity curve for the snake *Natrix natrix* was determined by Granit, employing an equal-energy spectrum, micro-electrode probes and a cathode-ray oscilloscope, and relying upon the electro-retinogram as an "indicator response" (Granit, 1947).

There are no behavioral studies on the color vision of Crocodilia available. In studying the iris response of the alligator, Laurens & Detwiler took the precaution of using an equal-energy spectrum. They found that the alligator has a Purkinje shift from a scotopic maximum of 514 millimicrons to a photopic one of 544 millimicrons. That part of the equal-energy spectrum which had a maximum effect on the iris response varies with the condition of the eye, being 544.2 millimicrons for the light-adapted eye, 504.4-514.3 for the dark-adapted eye (Laurens & Detwiler, 1921).

The experimental investigations outlined in the above may be evaluated from three points of view: a, the nature of the chromatic stimulus-variable; b, the method used in establishing a decisive indicator response; c, the systematic variation and control of brightness (Yerkes & Watson, 1911). These evaluative considerations will be treated in their respective order.

The Nature of the Chromatic Stimulus-variable. — Investigators employing various kinds of colored papers lay themselves open to a general criticism directed against such projects. Colored papers do not permit effective and adequate control of intensity, saturation and wave length. Further, the use of colored papers introduces other extraneous and uncontrollable factors such as surface reflectance, texture and irregularities in pigment coloration. Only those investigations which involve the use of spectral lights or filtered light are really worthy of consideration. If the retinal-sensitivity studies of Granit and Laurens, already noted, are excluded for the moment, then it can be said that only the work of Hess and Wojtusiak are of primary importance. All other researchers in this field used either Ostwald color papers, dyed food morsels or bits of tinted glass. Hess used prismatic light. Wojtusiak used Ostwald color papers in a preliminary study, and both filtered light and spectral light in his main study.

Hess presented food to turtles under light of various wave-lengths, believing that those wave-lengths under which turtles seized the food were visible to the animals and those under which they failed to take the food were invisible. He placed the animals and the food on a black mat and threw light, broken up into the spectrum by a prism, upon the food. The experimental subjects ate the food which lay in the red band. They also seized food in the yellow band, but neglected food illumined by all other wave bands. Hess concluded that his subjects could not see the blue end of the spectrum since they responded only to the red end. A subsequent series of tests employing color filters seemingly supported this conclusion.

In his preliminary work with Ostwald color papers, Wojtusiak found that turtles could be trained to distinguish grays only if their shades were markedly different. He also found that each of the colored papers could be distinguished from any of the seventeen grays. Wojtusiak's experimental subjects were able to discriminate twelve spectral lights. The spectral limits for the turtle were somewhere between 401 millimicrons and 760 millimicrons. Hues were most readily discriminated in the neighborhood of orange-red (634 millimicrons), with a weaker maximum of facility in discriminating in the region of blue-green (504 millimicrons) and violet, and a minimum in the blue. These latter sensitivity results are corroborated by the behavioral investigation of Bartkowiak (1949). He found that tortoises display a higher sensitivity to saturation differences in colors at the extreme ends of the spectrum, i.e., red and violet. They display a lowered sensitivity to saturation differences in the region of blue and green. Again, these results are substantiated by the well controlled investigation of Granit, who

used micro-electrodes and a cathode-ray oscilloscope in measuring retinal action currents activated by different wave lengths along an equal-energy spectrum (Granit, 1947).

Methods.—Methods refer essentially to the kinds of technique used in establishing the indicator response. These techniques may be subdivided into non-training methods and training methods. Non-training methods embrace preference methods, pupillary responses, adaptive responses such as color changes, respiratory responses and electro-retinogram responses. In the studies surveyed above, preference methods are to be found in the work of Hess (1910) and Hooker (1911). Pupillary responses are employed by Laurens (Laurens & Detwiller, 1921). Electro-retinogram responses are used by Granit (1947). Training methods refer to the use of instrumental act conditioning to establish the indicator response. Training methods appear in the work of Wojtusiak (1932), Wojtusiak & Mlynarski (1949), and in the work of Bartkowiak (1949), Kuroda (1933), Wagner (1932), Schlieper (1927), and Swiezawska (1949).

Training methods are usually regarded with more confidence in the testing of color vision capacities. Electrical techniques are of course the most exact, but these are not essentially behavioral techniques. Further, the results obtained do not necessarily correspond with the performance capacities of the experimental subject. In the case of the cat, for example, Granit reports positive results for the retinal, color vision capacities of this animal (Granit, 1947, p. 272). But Walls is unable to cite one behavioral study among the many conducted which might support the conclusion obtained using the micro-electrode technique and the electro-retinogram response (Walls, 1942, pp. 506-507).

Preference methods simply do not tell us anything about the range of the animal's capacities. They merely indicate that certain responses are performed with greater probability than other possible responses. Thus, in using the preference method, Hess erroneously concluded that, because tortoises seized food under colored light from the red end of the spectrum, they could not see or could not discriminate at the blue end. As is now known, the supposed preference for the red end is determined by a greater sensitivity to these wave lengths. The critical moment in the training procedure consists in getting the experimental animal to respond differentially. In some overt way, either by snapping, biting, clawing, rubbing or blowing, the experimental animal must prove to its trainer that it is capable of selecting the stimulus variable which is instrumental in bringing about the reinforcement. The indicator response which has proved to be most successful in working with tortoises is the snap-reaction or sham bite. This response features notably in the work of Wojtusiak, Wojtusiak & Mlynarski and Bartkowiak. It is also the indicator response employed in the present study.

Brightness Control.—The importance of controlling the brightness factor cannot be overestimated. It may very well happen that the chromatic stimulus variable, to which the animal is trained to respond positively, is consistently brighter or dimmer than the chromatic stimulus variable which the animal is trained to avoid. In such a case, the animal would be discriminating on the basis of brightness while seemingly discriminating on the basis of hue. The possibility of this kind of error would be greater for those animals having an intrinsic preference for the brighter or dimmer of any two stimuli. Walls cites evidence in support of this point (Walls, 1942, p. 510). Also, it should be noted that in the present study it was found that the experimental subjects first learned the brightness habit, and then the hue habit. The brightness habit had to be unlearned prior to establishing the hue habit.

The range of brightness values sampled should be extensive enough to insure adequate coverage of the animal's sensory capacities. In addition such factors as sensitivity-curve ratios make it essential that the range be wide enough to allow for a subjective equating of brightness measures somewhere along the continua which are being discriminated. If colored papers are used, the test would be between a color and a graded series of grays. If the animal becomes confused in discriminating between any of the chromatic-achromatic presentations, then presumably all prior discrimination was based on brightness cues. Brightness control carried out with a chromatic series and an achromatic paper series features in the work of Wojtusiak, Wojtusiak & Mlynarski, Bartkowiak, Kuroda, Swiezawska, Schlieper and Wagner.

If beams of light are used, then brightness control can be secured adequately by adopting the following procedure. First, one of the chromatic stimulus-variables is held constant at a predetermined value which will approximately bisect the range interval through which the alternate member of the discriminating pair is to be varied. The alternate member of the

pair is then varied in a systematic fashion in very small steps over a wide range of intensity values (from about three to five log units). In this way, not only is there assurance that the experimental animal has not been using brightness as a cue, but also there is presumptive reason for believing that the point of subjective equality has been crossed. That the point of subjective equality has actually been crossed can be established with certainty if predetermination of critical points are made with the aid of sensitivity curves. In none of the studies cited above is this kind of decisive control of the brightness factor adopted.

Preliminary Study

Before the main study on Giant Tortoises in the New York Zoological Park was undertaken, a preliminary study was made to determine whether the proposed experimental design was actually feasible.

Subjects were two specimens of Galapagos Giant Tortoise, *Testudo elephantopus vicina* Guenther, designated as T-1 and T-2. Apparatus consisted of several series of six-inch squares, on which were placed either colored papers or chromatic or achromatic pigment paints. The stimulus material was protected by a cellophane sheet on which was superimposed a sturdy Masonite frame, the cut-out of which allowed an actual surface area of 4″ × 4″ to be exposed to view. Approximately forty such panels were used during the course of experimentation. The stimulus panels were supported by brass hooks and were suspended from a heavy wire, strung at the eye-level of the experimental animal at a convenient corner of the interior pen of the tortoise shelter. The use of a right-angle portion of the interior pen for presenting the stimulus panels made it possible for the experimenter to offer two or more different visual stimuli simultaneously, while still being certain that the total stimulus situation was within the visual range of a given subject. Later on in the study, i.e., once conditioning to the experimental problem had been perfected, a shield was employed behind which the experimenter could move without fear of providing special sensory cues to the animal subject. Windows of an appropriate size were cut in the shield, through which the stimulus panels could be inserted and presented. Slide doors governed the opening and closing of the windows.

The experimental procedure may be treated under three headings: conditioning required to establish the indicator response, color-discrimination training and color-discrimination testing.

Conditioning Required to Establish the Indicator Response.—An experimental animal was tentatively selected from the herd of Giant Tortoises available. The experimental animal chosen (T-1) exhibited the kind of aggressiveness and active responsivity which seemed to be desirable in order to effect the conditioning of a possible set of indicator movements. This prediction of cooperative and successful performance was eventually realized in the course of experimentation. The snap-reaction or sham bite was soon discovered to be an adequate and decisive indicator response. Parenthetically, an indicator response may be defined as a definitive movement made in the direction of the positive stimulus, involving neuro-muscular change and sometimes a change in the orientation of the sensory receptors, especially the eyes and the ears. As noted, the indicator response developed in this study was the snap-reaction. In executing this response, the tortoise would extend its head and neck noticeably beyond the carapace and plastron, orienting the eyes and head in the direction of the reward color. The animal would then proceed to bite, without necessarily making tactual contact, at the colored surface just as if it were reaching for and snapping at food. The establishment of the indicator response was greatly facilitated by the fact that the animal seemingly displayed an unlearned propensity for biting and chewing as its own peculiar mode of exploring and modifying the environment. The marked orality of the tortoise provided the very promising lead as to what organ or group of organs, what neuro-muscular complex, might best be utilized in establishing a successful indicator response. The animal seemed to show from the beginning a strong preference for yellow and orange. Hence, the indicator response was conditioned positively to orange. It took between 200 and 300 trials to establish the indicator response to orange-colored paper alone for experimental subject T-1 and its co-subject, tortoise T-2.

The conditioning method employed may best be described as instrumental reward training. It is that form of learning in which the strengthened act, manipulative or locomotor, produces an unconditioned stimulus capable of satisfying a drive. In this instance, the execution of the sham bite in the direction of the positive stimulus (the strengthened act) was immediately followed by the application of the unconditioned stimulus (food reward or banana skin). The execution of the sham bite in the direction of the negative stimulus was unrewarded.

Table 1. Data for Initial Training and Testing Discrimination Tasks

Color-discrimination Task	Total Trials	Reward Color	Non-Reward	Percentage Success
Experimental Subject: T-1				
Orange-Blue	100	Orange	Blue	99
Orange-Green	100	Orange	Green	99
Blue-Green	100	Blue*	Green	90
Experimental Subject: T-2				
Orange-Blue	100	Orange	Blue	99
Orange-Green	100	Orange	Green	99
Blue-Green	100	Green†	Blue	92

* In the case of this animal, T-1, it required 30 trials to effect the shift from the reward color of orange to the reward color of blue.

† In the case of T-2, it required 24 trials to effect the shift from the reward color of orange to the reward color of green.

Color-discrimination Training.—An additional 100 trials were required to bring about successful differential responses between orange-colored paper and blue-colored paper in the case of animal subject T-1, and orange-colored paper and green-colored paper in the case of animal subject T-2. The measurement of performance for the various discrimination tasks reported was begun on the average of the end of 350 trials.[3]

Color-discrimination Testing.—The data for the initial discrimination task are given in Table 1, along with the related data for a second animal subsequently trained and tested. In the preliminary study, colored papers and pigment paints were used. Filtered light was not used. All colored papers were equated for surface brightness with the aid of a photometer.

After the training for Orange-Green and Orange-Blue discrimination had been completed and tested, an attempt was made to shift the reward color from orange to blue in the case of subject T-1, and from orange to green in the case of subject T-2. This shift was successfully accomplished with 30 trials for T-1 and within 24 trials for T-2. These data are reported in footnotes for Table 1. Later, the ability of the experimental animals to discriminate between a series of three blues in the case of T-1, and a series of three greens in the case of T-2, against a series of twenty grays, ranging in brightness from white to black, was tested. The members of the chromatic series were of different intensities and different saturations. These data are reported in Table 2. The spectrophotometric data for the chromatic series in question, and sample values for the achromatic series selected at regular intervals along the brightness continuum, are given in Table 3. The stimulus variables used here were pigment-paint, color surfaces.

Finally, the ability of the experimental animals to discriminate between a series of three blues of different intensities and different saturations, and a series of three greens of different intensities and different saturations, was determined. Spatial position and order of presentation were varied in a random way with the aid of a 9 × 9 non-orthogonal Latin Square (Fisher & Yates, 1949). These data are reported in Table 4. The stimulus variables used here were colored papers. The appropriate spectrophotometric data are given in Table 3.

The performance of T-1 on the visual discrimination task which provides the basis for Table 4 was retested after an eight-month interval of no practice. Retention was almost perfect. Only one error was recorded.

Table 2. Data for Chromatic vs. Achromatic (Pigment Paint) Discrimination Tasks

Color-discrimination Task	Total Trials	Reward Color	Percentage Success
Experimental Animal: T-1			
Blue #1, Blue #2, Blue #3 vs. Gray series	60	Blue	91.5%
Note: Errors were greatest for poorly saturated colors and for colors of low intensity; hence, greatest for Blue #3 and duller members of gray series. All errors checked in subsequent tests.			
Experimental Animal: T-2			
Green #1, Green #2, Green #3 vs. Gray Series	60	Green	85%
Note: Errors were greatest for poorly saturated colors and for colors of low intensity; hence, greatest for Green #3, and duller members of gray series. All errors checked in subsequent tests.			

[3] In this first series the Chi-square test of significance was applied in the attempt to evaluate the preliminary performance (Fisher & Yates, 1949; Lewis & Burke, 1949).

TABLE 3. SPECTROPHOTOMETRIC DATA

Percentage Spectral Reflectance in Visible Region of Different Gray Panels

Wave Length (mμ)	400	450	500	550	600	650	700	750
Gray #1	.365	.475	.550	.562	.575	.587	.600	.625
Gray #2	.275	.295	.300	.290	.280	.270	.265	.265
Gray #4	.165	.150	.137	.125	.115	.110	.105	.100
Gray #10	.110	.100	.088	.080	.075	.057	.070	.070
Gray #14	.080	.070	.065	.065	.060	.060	.050	.050
Gray #16	.080	.070	.065	.060	.055	.055	.055	.050
Gray #21	.045	.045	.040	.040	.040	.040	.035	.035

Spectral Reflectance in Visible Region of Different Color Panels
(Pigment Paint Panels and Paper Panels)

Wave Length (mμ)	400	450	500	550	600	650	700	750	Spectral Reflectance At. Maximum	Max. At. (mμ)
Green Pt. #1	.110	.062	.085	.150	.075	.100	.163	.300	.180	535
Green Pt. #2	.100	.065	.080	.125	.075	.088	.125	.162	.140	535
Blue Pt. #1	.062	.070	.060	.040	.038	.038	.045	.062	.075	470
Blue Pt. #2	.062	.065	.055	.045	.040	.040	.045	.055	.070	470
Green Paper #2	.075	.085	.225	.140	.065	.050	.060	.060	.235	510
Blue Paper #2	.290	.375	.000	.030	.025	.040	.150	.350	.380	445

The conclusion to be drawn from the preliminary study were:

1. *Testudo elephantopus vicina* shows a decided orange preference.

2. The principles of instrumental act conditioning are applicable to *Testudo elephantopus vicina.*

3. Retention in *Testudo elephantopus vicina* is exceptionally good and warrants the use of the species in continuing experimental tests.

4. The Galapagos Giant Tortoise can be retrained readily to new reward colors.

5. The Galapagos Giant Tortoise is capable of responding differentially among chromatic pairs of blue, green and orange papers.

As a result of this preliminary study, the author found himself in possession of two trained animals, and an indicator response had been isolated providing the basis for a conditioning procedure. It had, furthermore, been established that a section of banana skin would serve as an acceptable reward for the experimental animals.

MAIN STUDY

SUBJECTS

The experimental animals used in the definitive experiment, following the preliminary testing, were the two trained tortoises, T-1 and T-2, both *Testudo elephantopus vicina* Guenther, and a third animal, an adult male of the Indian Ocean species of Giant Tortoise, *Testudo gigantea* Schweigger, called T-3.

The gigantic land tortoises probably do not differ essentially in optical ability and structure from the numerous small species of the genus *Testudo* that occur in Europe, Asia, Africa and the western hemisphere (Van Denburgh, 1914).

The Chelonian Retina.—An excellent and adequate description of the chelonian eye as a whole is provided by Walls (1942, pp. 609-611). Of especial interest here is the chelonian

TABLE 4. DATA FOR BLUE SERIES VS. GREEN SERIES

Experimental Animal: T-1			
Color-discrimination Task	Total Trials	Reward Color	Percentage Success
Blue-Green	162	Blue	88%
Note: All errors checked in subsequent tests.			
Experimental Animal: T-2			
	81	Green	91%
Note: All errors checked in subsequent tests.			

retina. According to Walls, the retina is impure in its lamination, with every nuclear layer containing some elements which belong to some other level. Horizontal cells have ropy processes, and may have reverted to a non-conductive function. All or nearly all chelonians have an area centralis. Outside of this, the visual ganglion cell ratio is in the neighborhood of 2:1. Within the area centralis there is a lower summation ratio. A fovea has been claimed, and later authoritatively denied, for each of the several genera. The turtles are properly placed among the pure-cone reptiles. But they do possess droplet-free elements with heavy, cylindrical outer segments, morphologically identical with the rhodopsin-containing rods of birds. It is not certain whether these cells contain rhodopsin, but since they are most numerous in the light-avoiding turtles it is highly probable that they are physiologically rods, bearing several signs of cone ancestry (Walls, 1942, pp. 611-612).

A sensitivity curve for the retina of the tortoise is provided by Granit (1947). Granit used the electro-retinogram as an indicator of differential sensitivity.

During the final phase of experimentation, a specimen of *Testudo gigantea* Schweigger, designated as T-4, died. The eyes of the animal were removed, placed in a fixative solution of 10% formalin, and then subjected to histological examination.[4] This revealed numerous cone structures tipped with lighter elements representing the oil droplets mentioned by Walls (1942) and Detwiler (1943). Of unusual interest were elongated structures almost in the middle of the array of cones, not tipped with lighter elements and from all appearances morphologically similar to rods. These structures resemble similar structures described by Detwiler.

Apparatus

Apparatus consisted of: 1, an experimental dark room; 2, an optical system composed of three 500-watt projection lamps, together with parallel-light lenses, condenser lenses and milk-glass screens; 3, a brightness-control system of transformers, variacs, voltmeters and ammeters; 4, two sets of Eastman Kodak color filters.

The experimental dark room, the optical system and the intensity-control apparatus are described in greater detail below.

The Experimental Dark Room.—The dark room originally employed was a simple 4′ × 4′ × 4′ cubicle, fitted with a periscopic mirror and a door. Plate I, Figure 1, shows the experimental animal T-1 modeling his technique and orientation in responding to the chromatic pairs. In this instance, he is being rewarded through one of the two 6″ × 6″ apertures made accessible or inaccessible by a sliding door operated from the outside. In working with the other two experimental animals, T-1 and T-3 (especially T-1), it was found that the dimensions of the dark room had to be expanded. The dimensions of the second dark room were 9′ × 11′ × 5′.

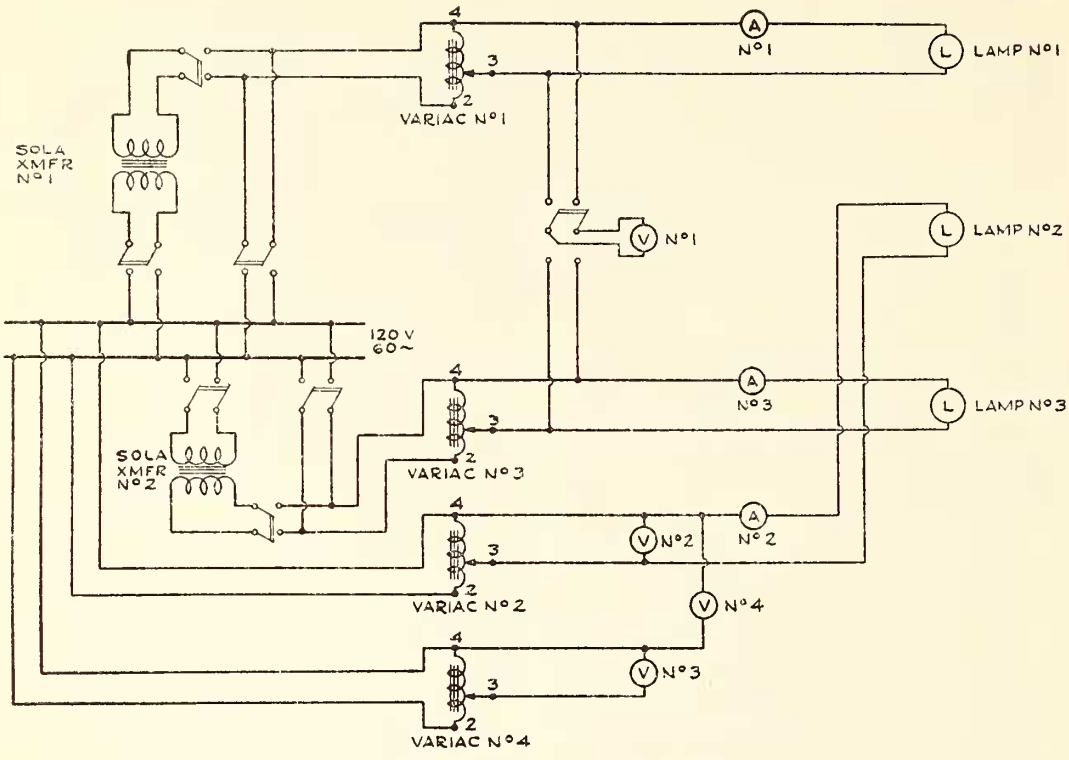
The Optical System.—The optical system is shown in Plate I, Figure 2, and Plate II, Figure 3. It will be seen that the optical system is composed of a series of three projection units mounted on a carriage which can be moved to the left or right depending upon the requirements of the random order adopted for left-right variations. In a typical experimental test, the two end projector-systems would carry the same kind of color filter—for example, green. The projection lamps in these two systems are held constant at a predetermined value. The center projection system carries a second color filter—for example, red. The luminance of the lamp in this system is the variable which is controlled by a variac, the latter being varied in .25 volt steps over a range of 20 volts to 105 volts. The use of three projector-systems arranged in the manner described made it possible to alternate stimuli positions to the left and right by shifting the carriage supporting all three projector systems. This device eliminates the need for an elaborate optical swivel arrangements for alternating constant and variable stimuli.

Brightness Control Apparatus.—A wiring diagram of the brightness control apparatus[5] with explanation of the electrical system is also given in Text-figure 1. A complete catalogue of instruments follows:

Variac #1	General Radio Co., Type V5 M T Range 0-130V, 50 to 60 cycles
#2	Rating—115V input 5a
#3	50 to 60 cycles
#4	General Radio Co., Type V5 MT Range 0-110V

[4] A 24-hour delay in carrying out the fixing procedures of the retina call into question precise accuracy of the sections obtained.

[5] The complicated brightness control system described in the above was employed instead of a wedge system for two reasons: 1) heat generated in the optical wedges by the large bulbs. 2) to conserve as much light energy as possible, it was decided not to use optical wedges, but rather a system of brightness control based on the use of variacs. Optical wedges will ordinarily cause a sacrifice of approximately 50 per cent of the original light energy.



TEXT-FIG. 1. Wiring diagram of intensity control apparatus.

Ammeter #1 Western Electrical Instrument Corp.
#2 Model 562 AC-DC
#3 Range 0-6 amps

Lamp #1 G.E. Mazda Lamp for picture projection
Code 500 T20/14-120V
#2 T-20 C-13 F Mog
500W-120V
#3 Calibrated

Voltmeter #1 Weston Electrical Instrument Corp.
Model 528 No. 51771
Range 0-150V AC
0-15V AC

Voltmeter #2 G.E. Range 0-150 AC Model VA X 5M

Voltmeter #3 Simpson Electric Co.
Range 0-150 AC Model 57

Voltmeter #4 Sensitive Research Instrument Corp., Mount Vernon, N. Y.
Multiple-Range Voltmeter
0-15 ⅛ Volt Steps
0-30 ¼ Volt Steps
0-50 ¼ Volt Steps
Model "D" No. 201287
Resistance 32.3 ohms per volt
Accuracy ¼%

Sola Transformer No. 1 and No. 2
Sola Electric Co.
Catalogue #4111
Primary Range 95-125V AC
Secondary Range 120 Volts Constant Amp 2.08
Frequency 60 cycle
Single Phase
Rated VA = 250

Variac No. 1 controls the intensity level of projection lamp No. 1. This system is monitored by ammeter No. 1 and voltmeter No. 1. A Sola transformer that can be cut in or out of the circuit is also shown. This instrument provides a current constancy of 99.9 per cent. Similarly, variac No. 3 controls the intensity level of projection lamp No. 3. This system is monitored by voltmeter No. 1 and ammeter No. 3. A simple switching system makes it possible to use voltmeter No. 1 for both projection lamps No. 1 and No. 3. The intensity level of projection lamp No. 2, the variable stimulus, is controlled by variac No. 2 and is monitored by ammeter No. 2 and voltmeters No. 3 and No. 4. The additional variac (No. 4) and voltmeters (No. 3 and No. 4) constitute a simple reading device for the very small voltage changes effected in projection lamp No. 2. The limited range of the sensitive voltmeter (50 volts) made it necessary to em-

ploy a circuit whereby the total range (20 to 105 volts) was divided to facilitate the measurement of successive .25 volt steps. In order to accomplish this, the center projection lamp was wired with a divided circuit. A secondary circuit was used to supply either 0, 30 or 60 volts. A primary circuit was used to bring this base voltage to the exact amount required. For the low voltages the primary circuit was used alone. For the middle voltages the auxiliary circuit was set at 30 volts. For the higher voltages the auxiliary circuit was set at 60 volts. In terms of the wiring diagram the constant voltage value measured by voltmeter No. 3 could thus be used as a base line against which increments effected by variac No. 2 and measused by voltmeter No. 2 could be read by the sensitive voltmeter (No. 4).[6]

Eastman Kodak Color Filters.—Filter Numbers 47 A-C5 (Blue), 61—N(Green) and 29—F (Red) were employed.

The spectrophotometric curves for these were calibrated by the Electrical Testing Laboratories.[7] Photometric brightness values at different voltage levels were calibrated for each of the color filters with the aid of a Macbeth Illuminometer. Chips taken from the filters actually being calibrated were inserted into the head of the Macbeth Illuminometer in order to facilitate matching of the brightness field of the Illuminometer with the brightness field of the test source. The resultant data are given in Table 5 for a first set. Values for a second set, not presented here, do not differ by more than 5 per cent from the values given for the first set. Photometric brightness values were in turn plotted against the corresponding voltage values for all three color filters. These functions are presented in Text-figure 2. The transmission values for the color filters were calibrated at a color temperature of 2360° K. Color temperatures in this study ranged upwards to 3100° K. It is to be noted, however, that a change in hue due to a change in color temperature of the test source is no greater than that often encountered when calibrating various kinds of white light with the Macbeth Illuminometer. Hence the accuracy obtained here is that usually obtained with the Macbeth Illuminometer.

[6] The help of Mr. Frank Alexandro of Ebasco Services, Inc., N. Y., and Prof. R. T. Weil of Manhattan College, N. Y., in the designing of the apparatus is hereby acknowledged.

[7] The Electrical Testing Laboratories, Inc., of 2 East End Avenue, New York 21, N. Y., is a commercial concern which conducts tests and supplies information on the accuracy, range of transmission of lights and light sources, filters, wedges, optical instruments and allied pieces of visual apparatus used commercially or in laboratory work.

Experimental Procedure

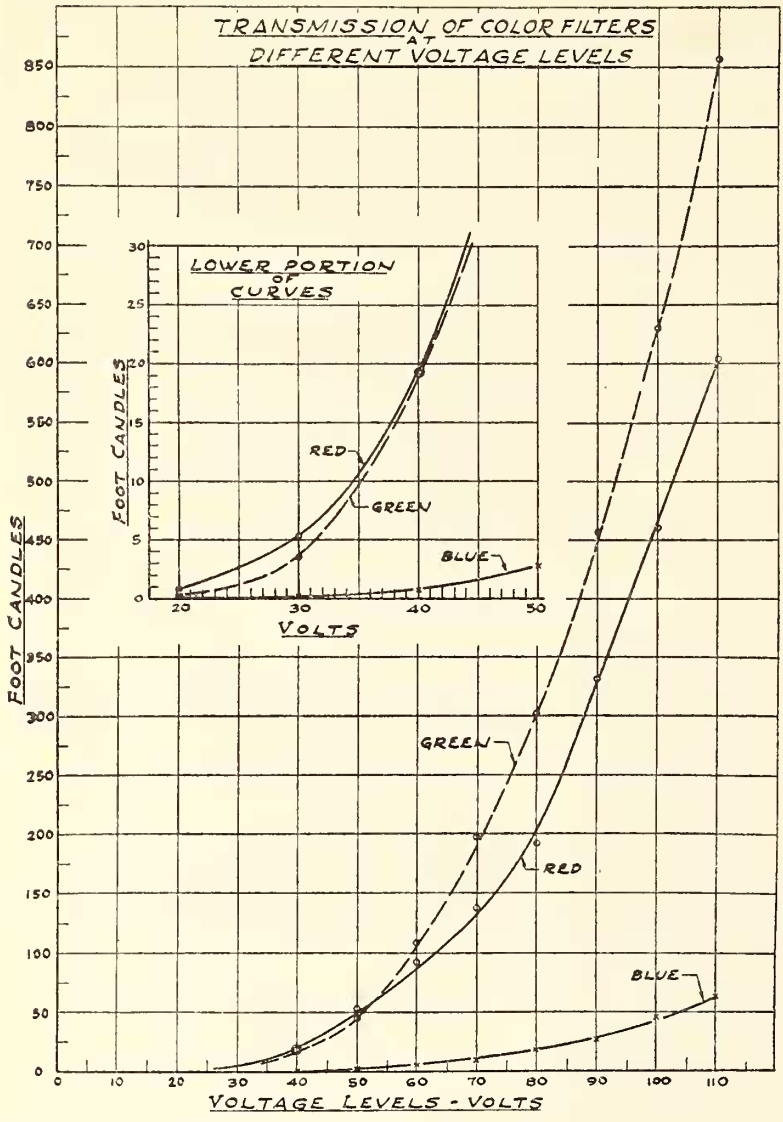
The experimental procedure to be described parallels very closely the procedure outlined by Warden, Jenkins & Warner in their discussion of an appropriate and adequate technique for determining the presence and quality of color vision in a new species (1936, pp. 172-173).

The first step in the color vision test is to establish a differential response to a pair of chromatic stimuli, or to a pair of stimuli consisting of one chromatic and one achromatic beam. This process is called establishing the "indicator response" and is essentially analogous to the learning technique referred to as "instrumental act conditioning." The indicator response in this instance consists in a kind of sham bite executed by the experimental animal and directed at the chromatic stimulus which has been arbitrarily selected as the "reward" stimulus.

After the response to the positive, chromatic stimulus has been established, control tests should be given. The control tests should be carried out as follows: a, hold the positive stimulus of the pair at the training intensity and vary the brightness of the negative stimulus in a systematic manner through a graduated series of intensity values; and, b, hold the negative stimulus of the pair at the training intensity and vary the brightness of the positive stimulus in a systematic manner through a graduated

Table 5. Relationship Between Voltage and Brightness, Calibrated with Aid of Macbeth Illuminometer

	Filter No. 47A—C5 (Blue)	Filter No. 61—N (Green)	Filter No. 29—F (Red)
Voltage	Brightness (ft.c.)	Brightness (ft.c.)	Brightness (ft.c.)
110	63.56	856.70	605.93
100	45.40	630.54	460.20
90	27.24	457.12	329.81
80	19.00	303.14	191.75
70	10.64	197.70	138.06
60	5.32	108.74	92.04
50	2.99	47.45	52.92
40	.98	19.11	19.18
30	.38	3.53	5.29
20	.04	.302	.92



TEXT-FIG. 2. Transmission of color filters at different voltage levels.

series of intensity values. The aim of this procedure is not to equate the brighness values of the two stimuli by matching them empirically, but to reverse the brightness values in the two stimuli so that these cannot be utilized as cues by the animal. On this account the range of intensity variations should be fairly wide, although it is hardly necessary that they extend over the entire intensity scale. In any case, the extent of the reversal must be sufficiently marked to rule out the possibility that brightness cues are effective. If the response to the positive chromatic stimulus is maintained throughout both control tests, the evidence for color vision may be accepted as conclusive, provided the experimental procedure in general has been properly carried out.

BASIC EXPERIMENTAL DESIGN

The basic experimental design consists in presenting chromatic stimuli which are held constant with respect to wave length, but which are varied alternately with respect to intensity over a wide range of brightness values (about 3 to 3½ log units). Right-left presentations for any one stimulus are also varied in a random way. Each of the experimental animals was conditioned positively to one of the primary colors, and negatively to all other colors. T-1 was conditioned positively to blue. T-2 was conditioned positively to green. T-3 was conditioned positively to red.

For one animal, T-2, an additional control was imposed. The reward color for T-2 was

shifted from Green to Red. Thus the original two discrimination tasks for T-2 were Red-Green (reward Green) and Blue-Green (reward Green). With the shifting of the reward color from Green to Red, it then became possible to test for Red-Blue discrimination (reward Red) and again, Red-Green discrimination (reward Green). The logic behind the imposition of the last control is simple. In the primary experimental design, checks were provided against intensity cues, spatial position cues and order of successive presentation cues by varying all three conditions randomly and systematically. The intrinsic preference value of a particular reward color was also controlled by conditioning a different experimental animal positively to each of the primary colors. This kind of control may be designated as inter-individual control of preference cues. In the secondary experimental design the same experimental animal is used as a check against itself. This kind of control may be designated as intra-individual control of preference cues. The ability of the experimental animal to utilize an entirely new set of cues in carrying out successful sequences of discrimination responses is conclusive proof of its discriminative capabilities.

It should be noted that the labels "condition I" and "condition II" are used to indicate not only discrete parts of the experimental design, but also the sequence of such parts. Condition I (vary the non-reward color) was usually followed by condition II (vary the reward color). This was not true for subject T-3. In that instance, condition I was alternated with condition II approximately every 100 trials. Actually no tortoise would continue to respond consistently and successively very much beyond 125 trials during any one experimental session. The cumulative effects of fatigue, waning of hunger motivation and reactive inhibition made it virtually impossible to test the subject beyond this limit. Usually the animal would recover after a 24-hour period of rest and food deprivation. Thus the complete testing of any one chromatic pair would take six sessions, each session lasting from two-and-one-half to three hours. The entire series of six sessions would be spaced over a period of about a week to ten days.

As already mentioned, animals were ordinarily deprived of food for a period of 24 hours. The exception to the rule was in the case of blue-green discrimination. A higher motivational level was required in order to effect sustained performance on the blue-green discrimination tasks. In this circumstance, animals were deprived of food for a period of two days to three days. The food reward which was supplied as reinforcement almost immediately following the execution of the desired response (snap-reaction) was a banana skin. Tortoises apparently have a strong predilection for this food, and a standard unit of reward was adopted approximately equivalent to ¼ of a full banana skin.

Results and Discussion

Prior to presenting the basic experimental data, it would be well to discuss in detail the rationale behind the determination of the "hold-constant" brightness values and "hold-constant" voltage values given in Tables 7-9. First, it was necessary to calibrate the photometric brightness values for each of the color filters at different voltage levels. As noted previously, this was done with the aid of the Macbeth Illuminometer. Matching of the brightness of the test source with the Macbeth field of brightness was facilitated by inserting a chip from the color filter which was actually being calibrated into the head of the Macbeth. These values were then plotted against the different voltages, yielding the functions given in Text-figure 2. Now, for any given chromatic pair, a "hold-constant" brightness value was selected which would approximately bisect the range of brightness values through which the alternate member of the pair would be varied. In this manner ample brightness space both above and below the "hold-constant" brightness value was provided in order to make it further possible to carry out adequate bracketing of the fixed value. It is to be emphasized that in employing this procedure, the experimenter in no way deluded himself into believing that the crossing of the probable points of subjective equality for the human retina was equivalent to the crossing of the probable points of subjective equality for the tortoise retina.

Table 6. Eastman Kodak Filters and Sensitivity Curve Factors for Human Retina and for Tortoise Retina (After Granit)

Color Filter	Maximum	Sensitivity of Human Retina Relative to Maximum	Sensitivity of Tortoise Retina to Equal Energy Spectrum at Corresponding Wave-Length
29FF Red Filter	650 mμ	.107	.600
61N Green Filter	530 mμ	.862	.500
47A Blue Filter	440 mμ	.023	.200

That the sensitivity curve factors for the human retina and the tortoise retina are not the same is well substantiated by Table 6. It is believed, however, that the ranges of brightness variation employed here are sufficiently extensive to insure the crossing of the points of subjective equality not only for the human retina but for the tortoise retina as well, somewhere along the continua of changing values. This last point receives additional weight when it is considered that the variability in differential sensitivity for the human retina is much greater than in the case of the tortoise retina. The human retina is approximately five times as sensitive to red as it is to blue. The ratio for the tortoise is three to one. The human retina is 37 times as sensitive to green as it is to blue. The ratio for the tortoise is two and one-half to one. The human retina is one-eighth as sensitive to red as it is to green. The ratio for the tortoise is one and two-tenths to one. In summary, it is affirmed that the probable points of subjective equality for the tortoise retina are contained within the limits of variation set up for the human retina. Direct determination of the critical values for the tortoise retina could only have been carried out had the original measurements been radiometric instead of photometric, and provided that more complete information concerning the differential sensitivity of the tortoise retina was available.

Tables 7. 8 and 9 give in schematic form the basic experimental design with accompanying brightness and voltage equivalences. Under column 1 is specified the information corresponding to "condition I" and "condition II." Under column 2 the brightness ranges and "hold-constant brightness values" are listed for each of the color filters and for each of the experimental conditions. Under column 3, the corresponding voltage values are given.

TABLE 7. SUMMARY OF VOLTAGE AND BRIGHTNESS EQUIVALENCES. COLOR DISCRIMINATION TASK: RED-BLUE

(1)	(2)	(3)
Experimental Design	Brightness Range for Human Eye (ft.c.)	Voltage Values
Vary Red	.92–506.22	20–105
Hold Blue Constant	27.24	90
Vary Blue	.04– 54.68	20–105
Hold Red Constant	12	35

TABLE 8. SUMMARY OF VOLTAGE AND BRIGHTNESS EQUIVALENCES. COLOR DISCRIMINATION TASK: BLUE-GREEN

(1)	(2)	(3)
Experimental Design	Brightness Range for Human Eye (ft.c.)	Voltage Values
Vary Green	.31–790.8	20–105
	3.53–790.8	30–105
Hold Blue Constant	27.25	90
Vary Blue	.40–54.68	20–105
	.38–54.68	30–105
Hold Green Constant	19.11	40

TABLE 9. SUMMARY OF VOLTAGE AND BRIGHTNESS EQUIVALENCES. COLOR DISCRIMINATION TASK: RED-GREEN

(1)	(2)	(3)
Experimental Design	Brightness Range for Human Eye (ft.c.)	Voltage Values
Vary Red	.92–506.22	20–105
	5.29–506.22	30–105
Hold Green Constant	35.1	46
Vary Green	.31–790.8	20–105
	3.53–790.8	30–105
Hold Red Constant	39.40	46

Tables 10 to 17 give the basic data for each of the experimental animals for each of the color discrimination tasks. The first line of data in each table may be taken as a brief résumé of the material which is reported in the body of the tables.

The response made by the animal upon the presentation of a discrete visual stimulus or of paired visual stimuli was tallied as one trial. It required approximately 300 trials to establish the indicator response in the case of animal subject T-3. An additional 200 trials (beyond the number already noted for establishing the indicator response) was needed to bring about successful differential responses between red colored paper and green colored paper. This animal was then shifted to the experimental dark room for testing with filtered light. Holding the brightness of the chromatic lights constant at predetermined levels, some 200 addi-

tional trials were found necessary in order to bring about sustained performance (at least 50-60 discrimination responses carried out successively).

No additional training in the experimental dark room beyond that given them in the pilot study was required for subjects T-1 and T-2.

It is to be noted that the errors reported represent initial deficiences in discriminating between chromatic lights. The data for the learning process involved in establishing the discriminative responses are given in Table 1. The errors reported here are errors in discrimination and not errors in learning. Although the preliminary learning data are interesting and informative, they actually bear no relevance to the discrimination data. All errors were corrected in subsequent trials by re-presenting the particular brightness levels that were unsuccessfully discriminated with an equal number of brightness levels that were successfully discriminated. Also worthy of mention is the fact that the distribution of errors in the case of each animal is random. There is no tendency for errors to cluster about any one point in the continuum of changing brightness values. On the other hand, there is a tendency for initial errors in the discrimination task to pile up in favor of the brighter of the two stimuli regardless of the chromatic pairs in question. In other words, the brightness habit had to be unlearned prior to establishing the hue habit.

With only one exception, the percentage error involved in the performance of the several discrimination tasks is never greater than 5 per cent. Again, with only one exception the percentage error reported is invariably higher, when the reward color is varied (condition II) as compared with the percentage error which arises under condition I—"hold-constant the reward color." Both exceptions occur in Table 15. The tendency for the animal to produce more errors when the reward color is varied than when it is held constant may simply mean that the tortoise, although discriminating on the basis of hue, finds it more difficult to respond to hue when the intensity of the stimulus in question is being continually and systematically changed. The two exceptions noted for subject T-2 in Table 15 may be readily explained by the fact that the reward color was shifted in the case of this animal from green (Tables 12 and 13) to red (Tables 14 and 15). The reversal of trend does not occur in Table 14 for subject T-2 simply because the particular color discrimination task (red-blue) does not bring out into the open the pro-active inhibitory influence of the previous "reward-Green" training. In Table 15 the trend is reversed because the particular color discrimination task in question does elicit the pro-active inhibitory influence of the earlier "reward-Green" training. Thus the total percentage error is not only highest in this instance, but also the trend of the sub-totals is reversed. Logically enough, the error trend for the sub-totals is in the direction of the earlier reward color, green—and for vary green (condition II).

Further analysis of the distribution of errors and successes apparently reveals no further trends. From the point of view of experimental efficiency, however, the color-discrimination task which proved to offer the greatest difficulty to the tortoise was the blue-green. This was even more marked under condition II, in which the reward color was varied, whether green or blue. That the tortoise could discriminate between blue and green is established by the fact that there is no unusual raising of the error level and by the fact that all errors were ultimately corrected. That blue-green discrimination offered greater difficulty to the tortoise is established by observations of the following:

1. Prolonged initial reaction time.
2. Prolonged total reaction time.
3. Frequent breaking with the problem. Subject T-1 discontinued all performance for a period of three weeks in the middle of his performance on this task. Subject T-2 took twice as long on this task as on any other save red-green discrimination, reward red.
4. Marked and frequent urination and defecation during the performance of the task.

The greater difficulty encountered by the tortoise in discriminating blue-green chromatic pairs is in agreement with the work of Wojtusiak and Bartkowiak. Bartkowiak found, for example, that within the field of red and violet the ability of tortoises in discriminating color-saturations from degrees of gray is greater than within the field of green, or especially blue (Bartkowiak, 1949). Similarly, the work of Wojtusiak shows that for the turtle, hues are most easily told apart when in the neighborhood of orange-red, with weaker maxima of discriminability at the blue-green and violet, and a minimum in the blue (Wojtusiak, 1932).

Summary and Conclusions

The present investigation was undertaken to determine the color vision capacities of the Giant Tortoise in discriminating among chromatic pairs of blue, green and red.

Subjects were two specimens of Galapagos Giant Tortoise, *Testudo elephantopus vicina* Guenther, and one specimen of an Indian

TABLES 10-13. EXPERIMENTAL DESIGN AND BREAKDOWN OF TOTALS FOR SUBJECTS T-1 AND T-2 ON DIFFERENT COLOR DISCRIMINATION TASKS

Subject: T-1 Species: *Testudo elephantopus vicinia* Guenther
Sex: Male Weight: 268 lbs.

TABLE 10. COLOR DISCRIMINATION TASK: RED-BLUE

Condition	Vary	Hold Constant	Total Trials	Errors	Success	% Error	% Success
I	Red 20-105 volts	Blue 90 volts	341	8	333	2	98
II	Blue 20-105 volts	Red 46 volts	341	17	324	5	95

TABLE 11. COLOR DISCRIMINATION TASK: GREEN-BLUE

Condition	Vary	Hold Constant	Total Trials	Errors	Success	% Error	% Success
I	Green 20-105 volts	Blue 90 volts	341	10	331	3	97
II	Blue 20-105 volts	Green 40 volts	341	17	324	5	95

Subject: T-2 Species: *Testudo elephantopus vicinia* Guenther
Sex: Male Weight: 343.5 lbs.

TABLE 12. COLOR DISCRIMINATION TASK: BLUE-GREEN

Condition	Vary	Hold Constant	Total Trials	Errors	Success	% Error	% Success
I	Blue 30-105 volts	Green 46 volts	301	3	298	1	99
II	Green 30-105 volts	Blue 90 volts	301	6	295	2	98

TABLE 13. COLOR DISCRIMINATION TASK: RED-GREEN

Condition	Vary	Hold Constant	Total Trials	Errors	Success	% Error	% Success
I	Red 30-105 volts	Green 46 volts	301	1	300	.3	99.7
II	Green 30-105 volts	Red 46 volts	301	2	299	.7	99.3

TABLES 14-17. EXPERIMENTAL DESIGN AND BREAKDOWN OF TOTALS FOR SUBJECTS T-2 AND T-3 ON DIFFERENT COLOR DISCRIMINATION TASKS

Subject: T-2 Species: *Testudo elephantopus vicinia* Guenther
Sex: Male Weight: 343.5 lbs.

TABLE 14. COLOR DISCRIMINATION TASK: RED-BLUE

Condition	Vary	Hold Constant	Total Trials	Errors	Success	% Error	% Success
I	Blue 20-105 volts	Red 35 volts	341	0	341	0	100
II	Red 20-105 volts	Blue 90 volts	341	4	337	1	99

TABLE 15. COLOR DISCRIMINATION TASK: RED-GREEN

Condition	Vary	Hold Constant	Total Trials	Errors	Success	% Error	% Success
I	Green 20-105 volts	Red 46 volts	341	29	312	9	91
II	Red 20-105 volts	Green 46 volts	341	18	323	6	94

Subject: T-3 Species: *T. gigantea* Schweigger
Sex: Male Weight: 275.5

TABLE 16. COLOR DISCRIMINATION TASK: RED-GREEN

Condition	Vary	Hold Constant	Total Trials	Errors	Success	% Error	% Success
I	Green 20-105 volts	Red 46 volts	341	4	337	1	99
II	Red 20-105 volts	Green 46 volts	341	19	322	6	94

TABLE 17. COLOR DISCRIMINATION TASK: RED-BLUE

Condition	Vary	Hold Constant	Total Trials	Errors	Success	% Error	% Success
I	Blue 20-105 volts	Red 35 volts	341	2	339	.6	99.4
II	Red 20-105 volts	Blue 90 volts	341	4	337	1.2	98.8

Ocean species of the Giant Tortoise, *Testudo gigantea* Schweigger. Microphotographs of histological sections of the retina of a specimen of *Testudo gigantea* Schweigger revealed the presence of a predominantly cone retina.

A preliminary study was conducted with two specimens of the Galapagos Giant Tortoise, employing colored papers of various brightnesses and saturations. In the main study, involving the use of filtered light, the experimental procedure for any one animal amounts to the following: Step I.—Hold the reward color constant at a brightness level which will be crossed by the range of brightness values through which the non-reward color will be varied. Vary the intensity (brightness) of the non-reward color in very small steps (.25 volts) over a wide range of predetermined values (from 20 to 105 volts). Step II.—Hold the non-reward color constant and vary the reward color in the manner already described. In this manner it was possible to provide two kinds of checks against brightness cues:

a. Brightness was varied in .25 volt increments over a wide range of values (from 3 to 3.5 log units). Presumably somewhere along the continua of changing brightness values for the chromatic pairs in question two stimuli were discriminated which in terms of the tortoise retina were approximately equivalent in brightness.

b. Systematic and extensive variation of brightness values probably provided assurance that brightness cues were not utilized in carrying out the successful discrimination sequences reported. Successive and progressive increment effects were avoided by adopting a random order of presenting the different brightness values.

Behavioral difficulty in discriminating blue-green pairs was observed and reported. This conclusion is in accordance with other experimental data (Bartkowiak, 1949; Wojtusiak, 1932).

In addition to the precautions adopted against brightness cues, this study differs from all other studies on reptiles in another respect. The positive stimulus for one of the experimental animals was shifted. In the particular case of subject T-2, the positive stimulus was shifted from green to red. This made it possible to test the full gamut of color combinations that can be arranged from the three primaries, blue, green and red. Also, this procedure ruled out the possibility that preference cues of some kind may have been operative in the discriminative performance of the animal.

Approximately 1,300 trials for any one color combination of chromatic pairs (red-green, red-blue and blue-green) were required to test the full number of intensity variations for the voltage ranges specified. Percentage success varied from 91% to 100%. All unsuccessful discriminations were subsequently retested with an equal number of previously-tested successful discriminations. All discriminations were ultimately successful.

The clear-cut results obtained in this study make it extremely difficult to call into question the color vision capacities of the Giant Tortoise, at least in discriminating among chromatic pairs of blue, green and red.

It is believed that the experimental evidence gathered here provides support at the behavioral level for Granit's hypothesis that animals showing modulator curves actually discriminate color.

Bibliography

Barnes, N. F.
1939. A Spectrophotometric Study of Artists' Pigments. Technical Studies in the Field of the Fine Arts. (Harvard University), 7: 120-138.

Bartkowiak, W.
1949. The Ability of Tortoises to Discriminate Color Saturations. Bulletin International de l'Academie Polonaise des Sciences et des Lettres. No. 1, January-March, 21-58.

Beebe, W.
1924. Galapagos, World's End. New York, G. P. Putnam's Sons. Ch. IX: Giant Tortoises, 204-229.

Boulenger, O. A.
1889. Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum.

Detwiler, S. R.
1943. Vertebrate Photoreceptors. New York, Macmillan Co.

Evans, Ralph, M.
1948. An Introduction to Color. New York, John Wiley & Sons.

Fisher, R. A.
1946. Statistical Methods For Research Workers (10th ed.). Edinburgh, Oliver and Boyd.

Granit, R.
1947. Sensory Mechanisms of the Retina. New York, Oxford University Press, pp. 266-297.

Hess, C. von.
1910. Untersuchungen über den Lichtsinn bei Reptilien und Amphibien. Pflügers Arch., 132: 255-295.

Hooker, D.

1911. Certain Reactions to Color in Young Loggerhead Turtles. Carn. Inst. Pub., Washington, D. C., 132: 71-76.

Kuroda, R.

1933. Studies on Visual Discrimination in the Tortoise, *Clemmys japonica,* Acta. Psychol. Keijo, 2: 31-59.

Laurens, H. & S. R. Detwiler.

1921. The Structure of the Retina of *Alligator mississippiensis* and its Photomechanical Changes. J. Exp. Zool., 32: 207-234.

Lewis, D. & C. J. Burke.

1949. The Use and Misuse of the Chi-Square Test. Psychol. Bull., 46: 433-489.

Rothschild, L.

1931. Exhibition of Specimen of the Saddle-Backed Races of Galapagos Tortoises. Proc. Zool. Soc. London, p. 1208.

Schlieper, C.

1927. Farbensinn der Tiere und Optomotorische Reaktionen. Zeits. f. Vergl. Physiol. Bd. 6, 453-472.

Swiezawska, K.

1949. Color-discrimination of the Sand Lizard, *Lacerta agilis* L. Bulletin International de l'Academie Polonaise des Sciences et des Lettres. No. 1, January-March. 1-20.

Van Denburgh, J.

1914. The Gigantic Land Tortoises of the Galapagos Archipelago. Expedition of the California Academy of Sciences to the Galapagos Islands, 1905-1906. Vol. II, Pt. I, 203-374, Sept. 30, 1914. San Francisco, California Academy of Sciences, 1914.

Wagner, H.

1932. Über den Farbensinn der Eidechsen. Zeits. f. Vergl. Physiol., Bd. 18, 378-392.

Walls, G. L.

1942. The Vertebrate Eye and Its Adaptive Radiation. Michigan, Cranbrook Institute of Science.

Warden, C. J., T. N. Jenkins & L. H. Warner.

1936. Comparative Psychology. New York, Ronald Press. Vol. I: Principles and Methods. Vol. III: Vertebrates.

Wojtusiak, R. J.

1932. Über den Farbensinn der Schildkröten. Zeits. f. Vergl. Physiol., Bd. 18, 393-436.

Wojtusiak, R. J. & M. Mlynarski.

1949. Investigations on the Vision of Infra-Red in Animals. II. Further Experiments on Water Tortoises. Bulletin International de l'Academie Polonaise des Sciences et des Lettres. Nos. 1-3, 95-120.

Yerkes, R. M. & J. B. Watson.

1911. Methods of Studying Vision in Animals. Behavior Monographs, 1, No. 2.

EXPLANATION OF THE PLATES

Plate I

Fig. 1. Giant Tortoise in darkroom, receiving reward.

Fig. 2. Side view of optical system, composed of three projection units mounted on carriage, illustrating relative positions of lamp, lenses and color filter. Cover of one unit removed.

Plate II

Fig. 3. Rear view of optical system. In the background is the slide door of the experimental darkroom.